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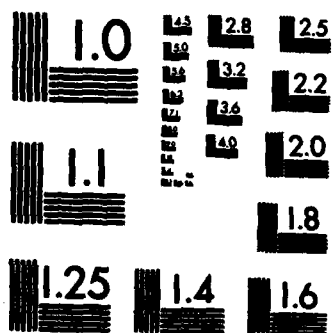
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20. ABSTRACT (Continue on reverse side if necessary and identify by block number)
The object of our research is to find principles of development and organization of neural networks that can account both for experimental data on the cellular level and, when applied to large numbers of neurons that receive sensory and/or interneuronal information, for various higher level systems properties. Networks of neurons already have been constructed that can organize themselves to display some cognitive properties. Although these are still primitive compared to what animals

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or even machines in some cases can presently do, it is of significance that these networks are self-organizing, that the global cognitive properties are the result of local modifications of the network components -- learning (so to speak) on a cellular level. This learning comes about through the modification of synaptic junctions (connections) between neurons. One crucial hypothesis concerns the form of this synaptic modification by applying them to the development of selectivity and ocular dominance in cat visual cortex, where much experimental data has been obtained in the last twenty years. This leads to a theory of synaptic evolution based on sets of coupled non-linear stochastic differential equations. Analysis and computer simulations show this theory is in good agreement with classical experimental results. In addition we obtain some new predictions that can be tested.

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A Model for the Development of Neurons

in Visual Cortex*

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Great attention has been lavished on the visual system in the last generation--and rightly so. For this system may provide a clue as to the means by which information is processed on its path from the sensory apparatus to 'higher' brain centers. But as is suggested in a large number of 'deprivation' experiments--experiments in which the normal development of visual cortex is modified by abnormal visual experience--the visual system may also provide a means of testing neuron learning on a single cell level.

For the visual system, we can control the dominant input, (in development as well as in testing) as well as measure the output. This gives us the possibility of measuring the change of response of individual neurons as a function of the sensory environment in which they are placed-assuming that what is observed in altered visual environments such as monocular deprivation or dark rearing are changes in responses of individual neurons rather than responses of different populations of neurons. Although it seems likely that this is indeed the case, the question will probably be settled finally by appropriate chronic experiments.

Even though such neuron learning may play only a minor role in contributing to the architecture of visual cortex, with a minimum of fortune, it could be related to learning that must take place in higher brain centers. It is this point of view that we have explored over the past few years.

Here d_ℓ, d_r, m_ℓ, m_r are inputs and synaptic junctions from left
and right eyes. The output of this neuron (in the linear region) can
be written

$$c = m_\ell \cdot d_\ell + m_r \cdot d_r \tag{1}$$

This means that the neuron firing rate (in the linear region) is the
sum of the inputs from the left eye multiplied by the appropriate
left-eye synaptic weights plus the inputs from the right eye
multiplied by the appropriate right-eye synaptic weights. Thus the
neuron integrates signals from the left and right eyes.

According to the theory presented by Bienenstock, Cooper and Munro,
1982 (BCM) these synaptic weights modify as a function of local and
global variables. To illustrate we consider the synaptic weight m_j
(figure 1b).

Fig. 1b

Local and Quasi-Local Variables

Its change in time, $\dot{m}_j$, can be written very generally as:

$$\dot{m}_j = F(d_j \cdot m_j; d_k \ldots c; \bar{c} \ldots; X, Y, Z). \tag{2}$$

Cortical neurons receive afferents from many sources. In visual cortex
(layer 4, for example) the principle afferents are those from the
lateral geniculate nucleus and from other cortical neurons. This leads
to a complex network that we have analyzed in several stages.

In the first stage we consider a single neuron with inputs from both
eyes (Figure 1a).

Fig. (1a)

A Model Neuron

Here variables such as d_j ... m_j are designated local. These represent information (such as the incoming signal, d_j, and the strength of the synaptic junction, m_j) available locally at the synaptic junction, m_j . Variables such as d_k ...c are designated quasi-local. These represent information (such as c, the firing rate of the cell, or d_k , the incoming signal to another synaptic junction) that is not locally available to the junction m_j but is physically connected to the junction by the cell body itself--thus necessitating some form of internal communication between various parts of the cell and its synaptic junctions. Variables such as $\bar{c}$ (the time averaged output of the cell) are averaged local or quasi-local variables. Global variables are designated X,Y,Z... These latter represent information (e.g. presence or absence of neurotransmitters such as norepinephrine or the average activity of large numbers of cortical cells) that is present in a similar fashion for all or a large number of cortical neurons (distinguished from local or quasi-local variables carrying detailed information that varies from synapse to synapse).

In a form relevant to this discussion, BCM modification is written

$$\dot{m}_j = \phi(c, \bar{c}; X, Y, Z...)d_j \tag{3}$$

so that the jth synaptic junction, m_j, changes its value in time as a function of quasi-local and time-averaged quasi-local variables, c and $\bar{c}$, as well as global variables X,Y,Z, through the function, ϕ, and a function of the local variable d_j. The crucial function, ϕ, is shown in Figure 1c.

Fig. 1c

The BCM Modification Function

What is of particular significance is the change of sign of ϕ at the
modification threshold, Θ_M, and the non-linear variation of Θ_M with
the average output of the cell, $\bar{c}$. In a simple situation

$$\Theta_M = (\bar{c})^2 \tag{4}$$

The occurance of negative and positive regions for ϕ drives the cell
to selectivity in a 'normal' environment. This is so because the
response of the cell is diminished to those patterns for which the
output, c, is below threshold (ϕ negative) while the response is
enhanced to those patterns for which the output, c, is above threshold
(ϕ positive). The non-linear variation of the threshold with the
average output of the cell, $\bar{c}$, places the threshold so that it
eventually separates one pattern from all of the rest. Further it
provides the stability properties of the system.

A detailed analysis of the consequences of this form of modification is
given in BCM. To illustrate we consider the various final states for
the cell under rearing conditions characterized as follows:

Normal Environment: The inputs from the eye are a stochastic sequence of patterns possibly distorted by noise (these patterns represent the mapping by retinal and LGN cells of images or patterns viewed by the animal). In normal rearing it is presumed that certain patterns (edges, for example) are a repeated part of the environment and are viewed by the animal many times. It is assumed that such patterns may be distorted or may appear in various combinations but that for a normal environment the patterns are statistically independent.

Restricted or Altered Environment: The inputs are restricted to one or a few patterns that may be highly correlated. This represents the mapping in the neural space of a restricted or artificial environment (for example, one in which only vertical lines or right angles are present).

Dark Reared Environment: The patterned inputs are replaced by random noise that represents the non-patterned input due to dark discharges and spontaneous activity of the retinal cells.

Various rearing conditions can then be represented as follows:

Normal Binocular Rearing:

Correlated patterns input from both eyes. This means that both the left and right eye see the same pattern at the same time.

Strabismic Rearing:

Non-correlated pattern input from both eyes. In this case the left and right see different patterns at the same time.

Monocular Deprivation: (right eye deprived)Patterned input from left eye. noise from right eye. In this case the left eye sees a pattern while the right eye is closed.

Binocular Deprivation:

In this case, both eyes being closed (or kept in the dark) noise is received from both eyes.

The consequences of the BCM modification in these classical rearing conditions are shown in Figure 2.

Fig. 2

Computer simulations of various rearing conditions. Initial

(dashed) and final (solid) responses to the two eyes are

shown separately (left/right).

These may be summarized as follows:

Monocularly driven neurons

(1) A monocularly driven neuron in a "normal" (patterned)
environment becomes selective. The precise pattern to which it becomes
selective is determined at random if there is no initial preference or
may be biased toward a particular pattern if there is a built-in preference
for this pattern.

(2) This same neuron in various deprived environments evolves as
follows.

PURE NOISE. The neuron becomes less selective but continues to be
(somewhat) responsive. It may show an orientation preference, but this
is relatively unstable.

EXPOSURE TO A SINGLE PATTERN (such as vertical lines). The neuron comes
to respond preferentially to the single pattern but with less selectivity
(less sharply tuned) than if all orientations were present in the environment.

(3) Inhibitory synapses are required to produce maximum selectivity.
If such inhibitory connections are arbitrarily set equal to 0, selectivity
diminishes.

Binocularly driven neurons

(1) A binocularly driven neuron in a "normal" (patterned) environment becomes selective and binocular. It is driven selectively by the same pattern from both eyes.

(2) This same binocularly driven neuron in various deprived environments evolves as follows.

UNCORRELATED PATTERNED INPUTS TO BOTH EYES. The neuron becomes selective, often monocularly driven; if the neuron is binocular, sometimes it is driven by different patterns from the two eyes.

PATTERNED INPUT TO ONE EYE, NOISE TO THE OTHER (monocular deprivation). The neuron becomes selective and generally driven only by the open eye. There is a correlation between selectivity and binocularity. The more selective the neuron becomes, the more it is driven only by the open eye. A non-selective neuron tends to remain binocularly driven. This correlation is due, in part, to the fact that it is the same mechanism of synaptic change that serves to increase both the selectivity and ocular dominance of the open eye. However there is also a subtler connection: it is the non-preferred inputs from the open eye accompanied by noise from the closed eye that drive the neuron's response to the closed eye to zero.

NOISE INPUT TO BOTH EYES (dark rearing or binocular deprivation). The neuron remains non-selective (or loses its selectivity) and diminishes its responsiveness but remains binocularly driven (in contrast to the situation in monocular deprivation).

An unexpected consequence of this theory is a connection between selectivity and ocular dominance. The analysis given in BCM leads to the conclusion that the more selective a cell is, the more the state of the closed eye will be driven to zero, so that the cell will be more monocular. Thus, during cell development, pattern selectivity for the open eye is achieved before the cell becomes monocular as Figure 3.

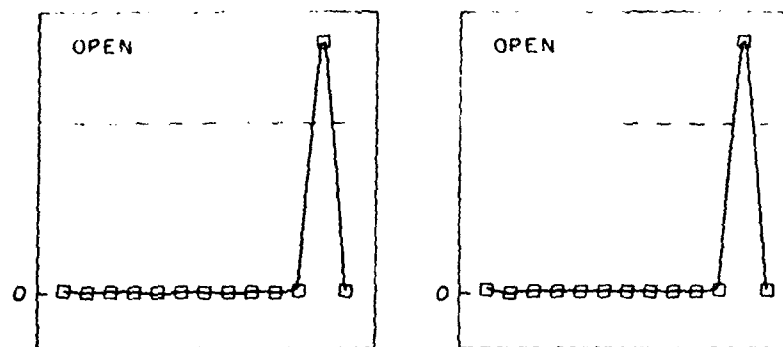Figure 3. Progression of development of selectivity and ocular dominance. Note that selectivity develops for the open eye before the response to the closed eye is driven to zero.

Since non-preferred inputs presented to the open eye are a necessary part of the suppression of deprived eye responses, if inputs to the open eye are restricted to preferred patterns, selectivity may still develop but the cell will be less selective to the open eye and less monocular than it would be in a non-restricted environment. Such effects should be experimentally observable.

To better confront these ideas with experiment a second stage of analysis is necessary. The BCM neuron must be placed in a network with the anatomical features of visual cortex; a network in which inhibitory and excitatory cells receive input from LGN and from each other. This has been done (Scofield and Cooper to be published). Our conclusions are similar to those of BCM with explicit further statements concerning the independent effects of excitatory and inhibitory neurons on selectivity and ocular dominance. For example. shutting off inhibitory cells lessens selectivity and alters ocular dominance. (masked synapses). These inhibitory cells may be selective but there is no theoretical necessity that they be so. Further the intra-cortical inhibitory synapses do not have to be very responsive to visual experience. Most of the learning process can occur among the excitatory LGN-cortical synapses.

Quantitative tests of progressions such as those shown in Figure 3 are in progress in our laboratory. We hope that such experiments can provide detailed comparisons of theory and experiment and provide us with a sensitive tool for determining synaptic modification among various classes of neurons--a possible entry to the process by which the nervous system organizes itself.

FIGURE CAPTIONS:

Figure 1a: A Model Neuron.

Figure 1b: Local and Quasi-Local Variables.

Figure 1c: The BCM Modification Function.

Figure 2:   Computer simulations of various rearing conditions.
               Initial (dashed) and final (solid) responses to the two
               eyes are shown separately (left/right). In this figure, NR
               means normally reared, BD means binocular deprivation, MD
               means monocular deprivation and RS means reverse suture.

Figure 3:   Progression of development of selectivity and ocular
               dominance. Note that selectivity develops for the
               open eye before the response to the closed eye is
               driven to zero.

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OPEN   CLOSED

Initial

OPEN   CLOSED

Intermediate

OPEN   CLOSED

Final

(a) NR

(b) BD

(c) MD

(d) RS

$d_\ell(t)$

$d_r(t)$

$m_\ell(t)$

$m_r(t)$

c

$$c(t)$$

$$m_k(t)$$

$$m_j(t)$$

$$d_k(t)$$

$$d_j(t)$$

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Initial

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$$c(t)$$

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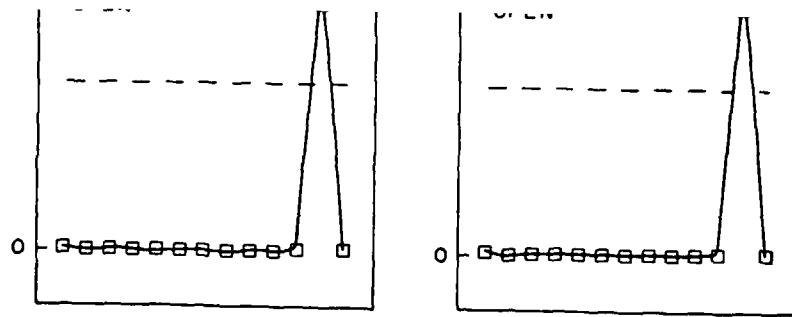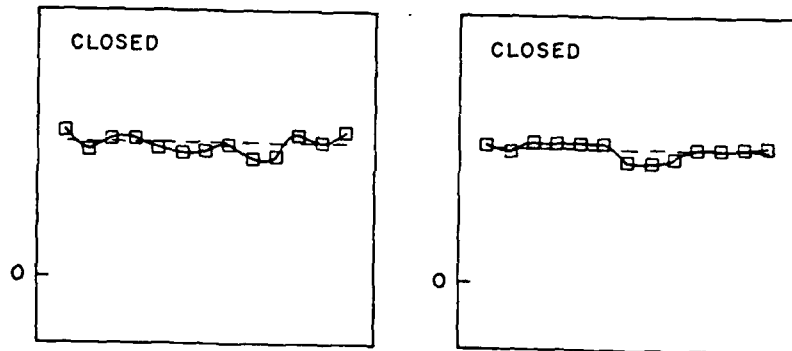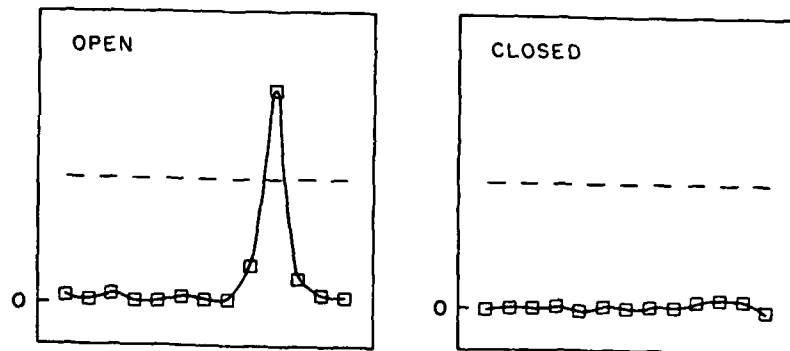
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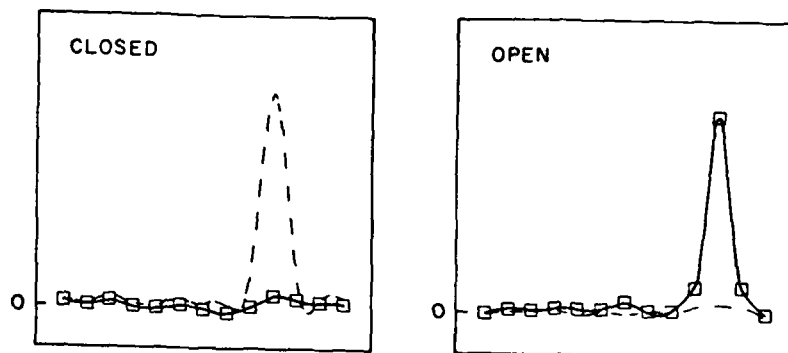
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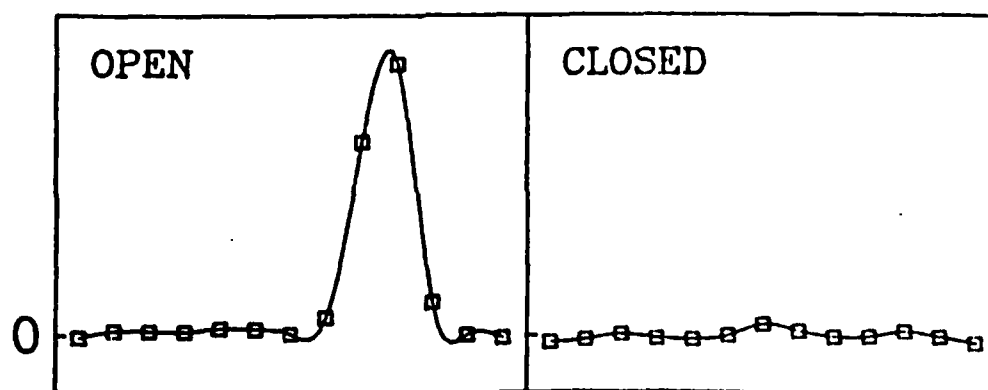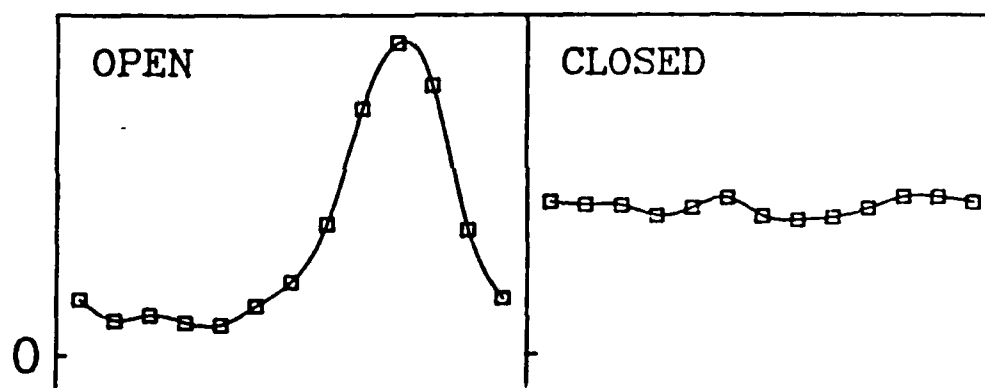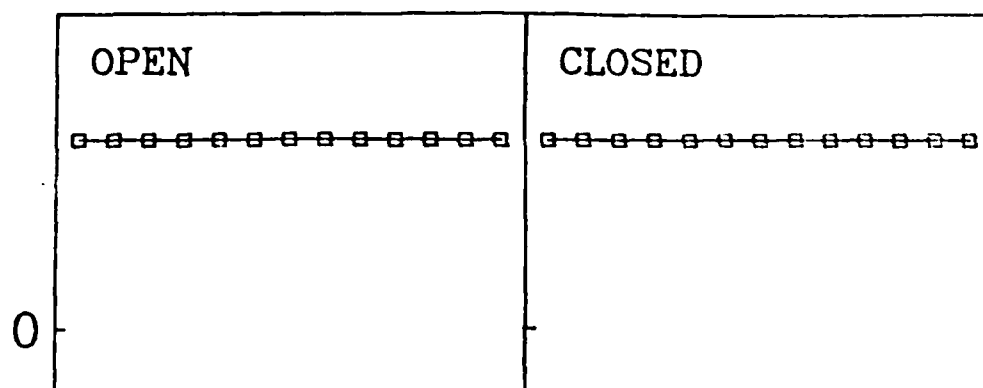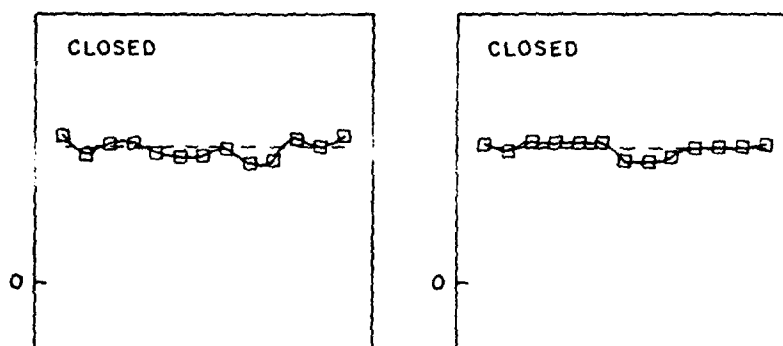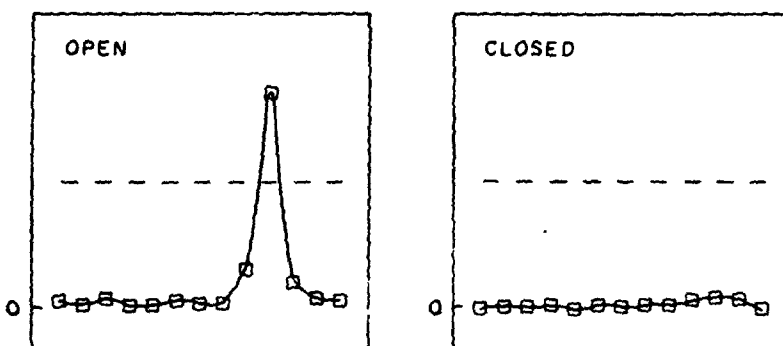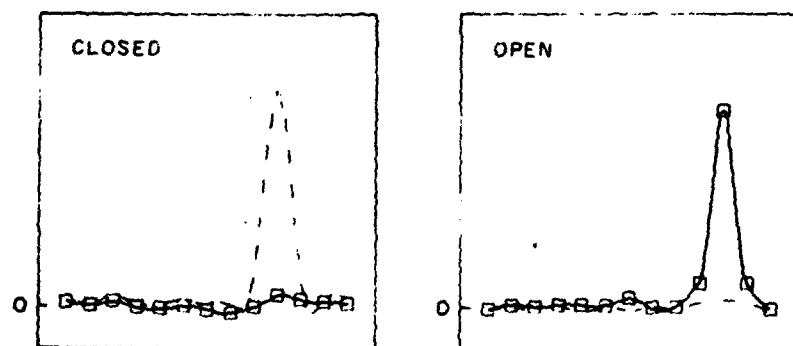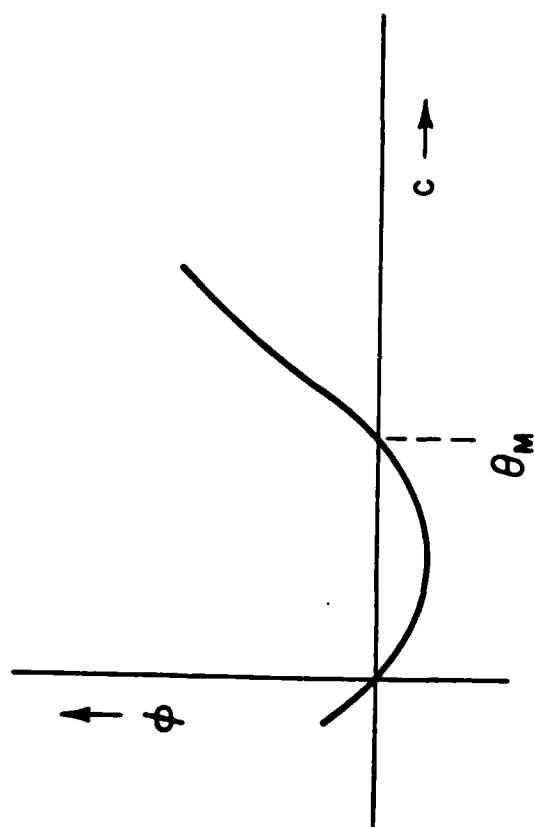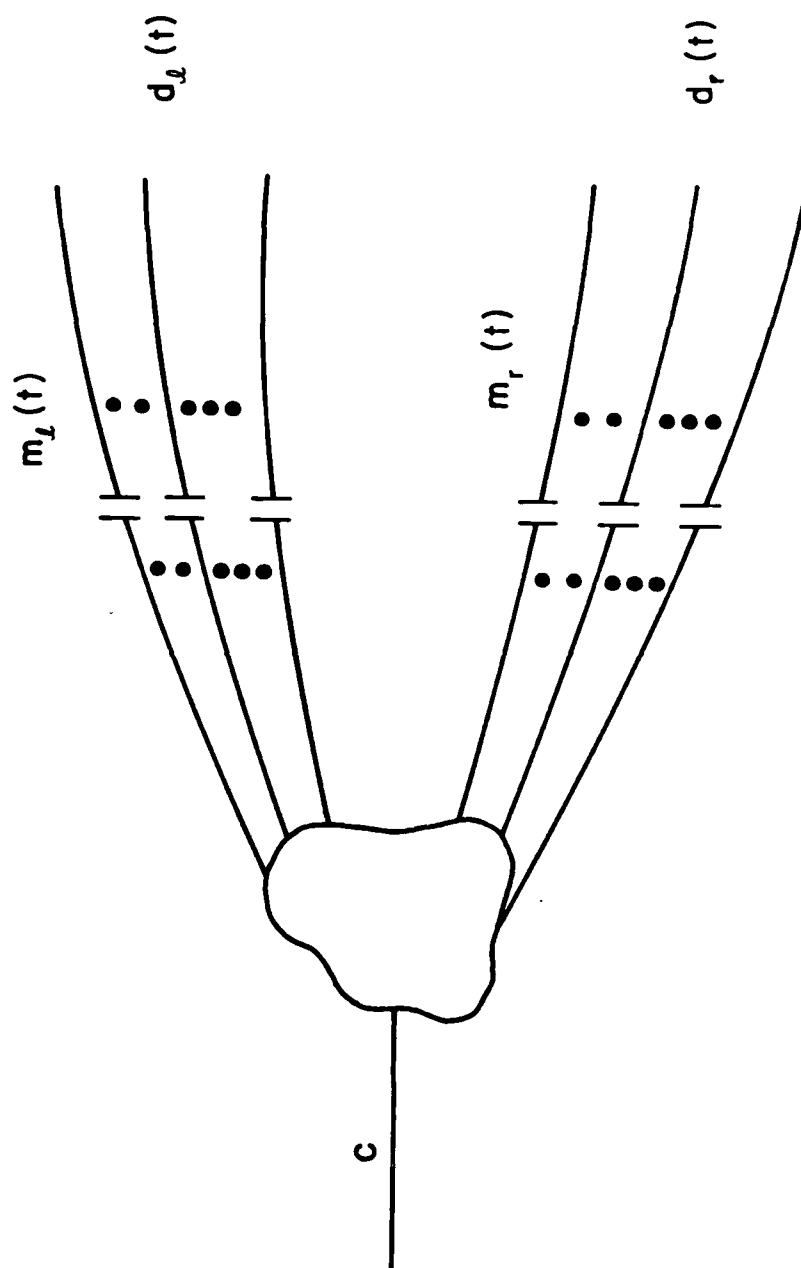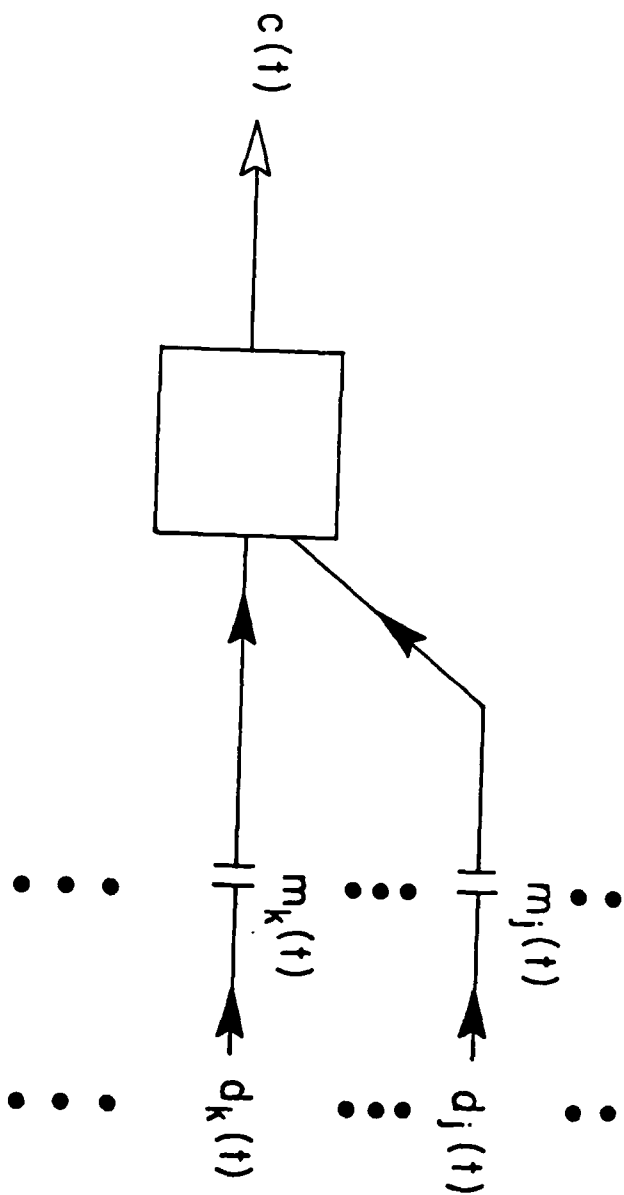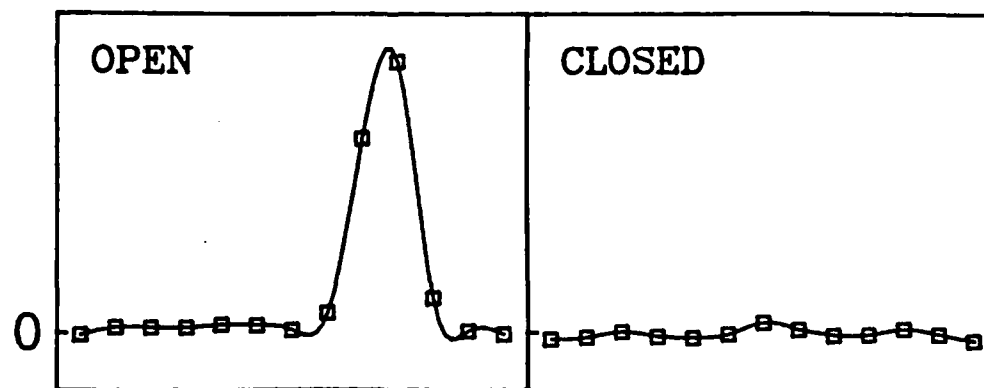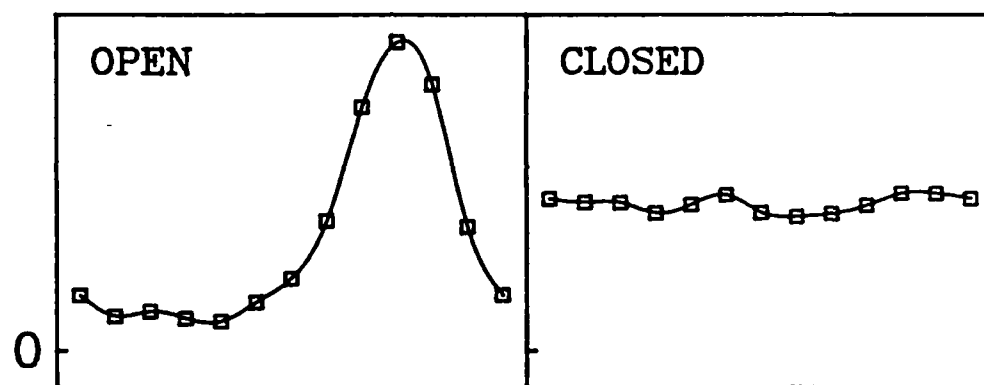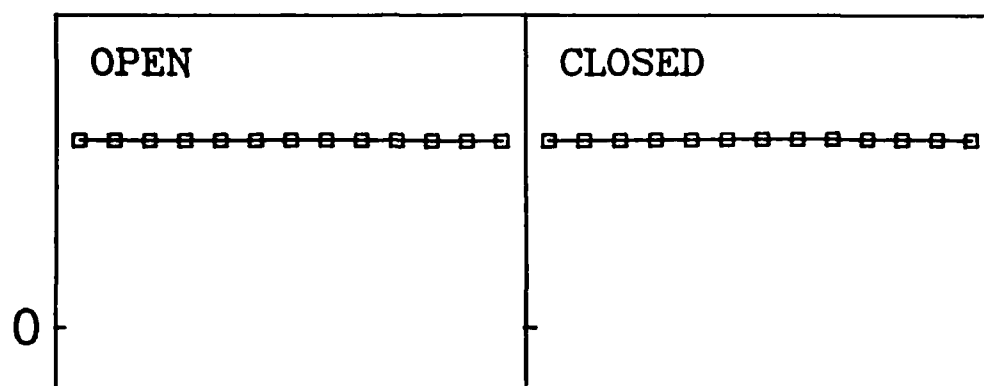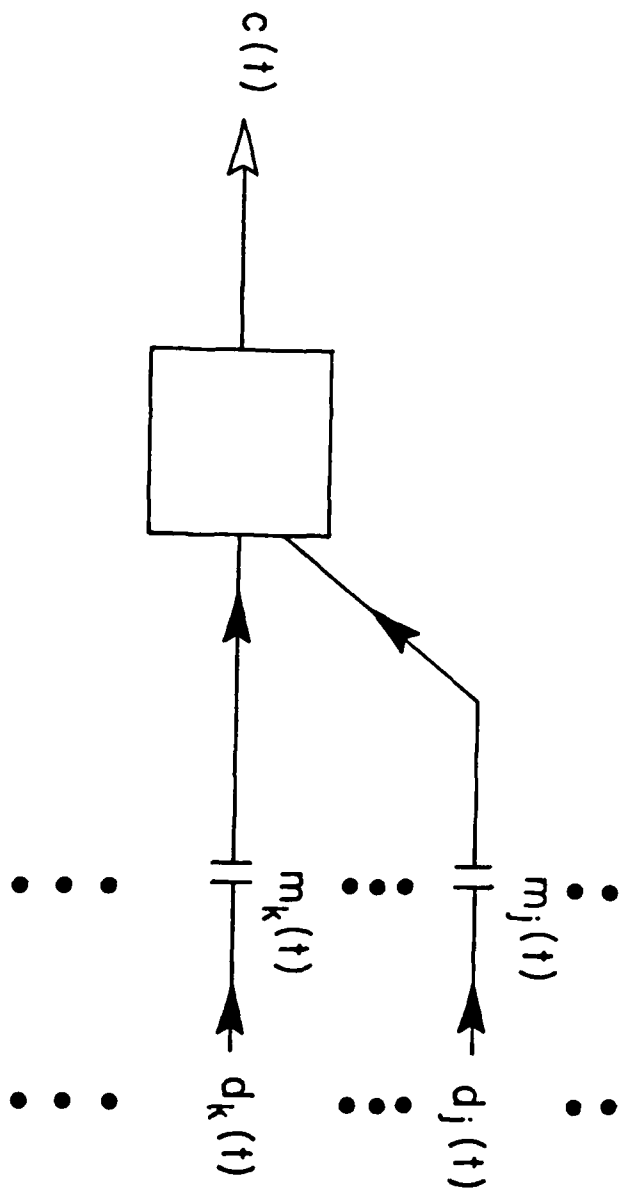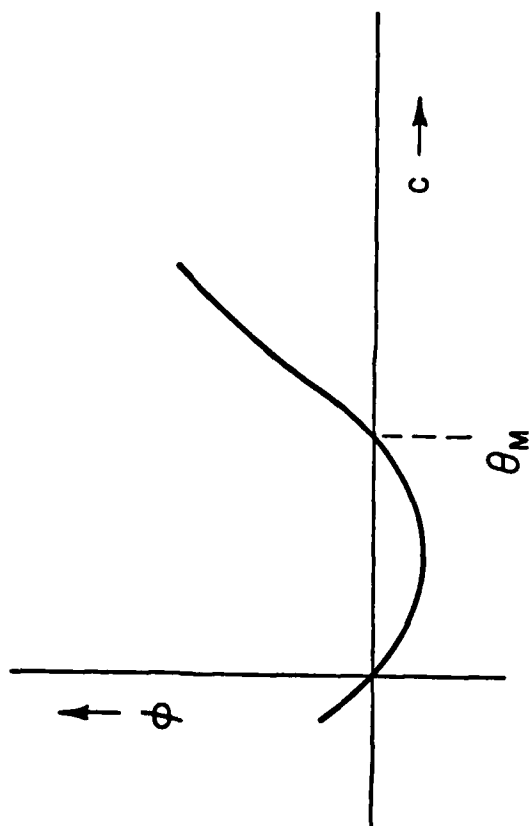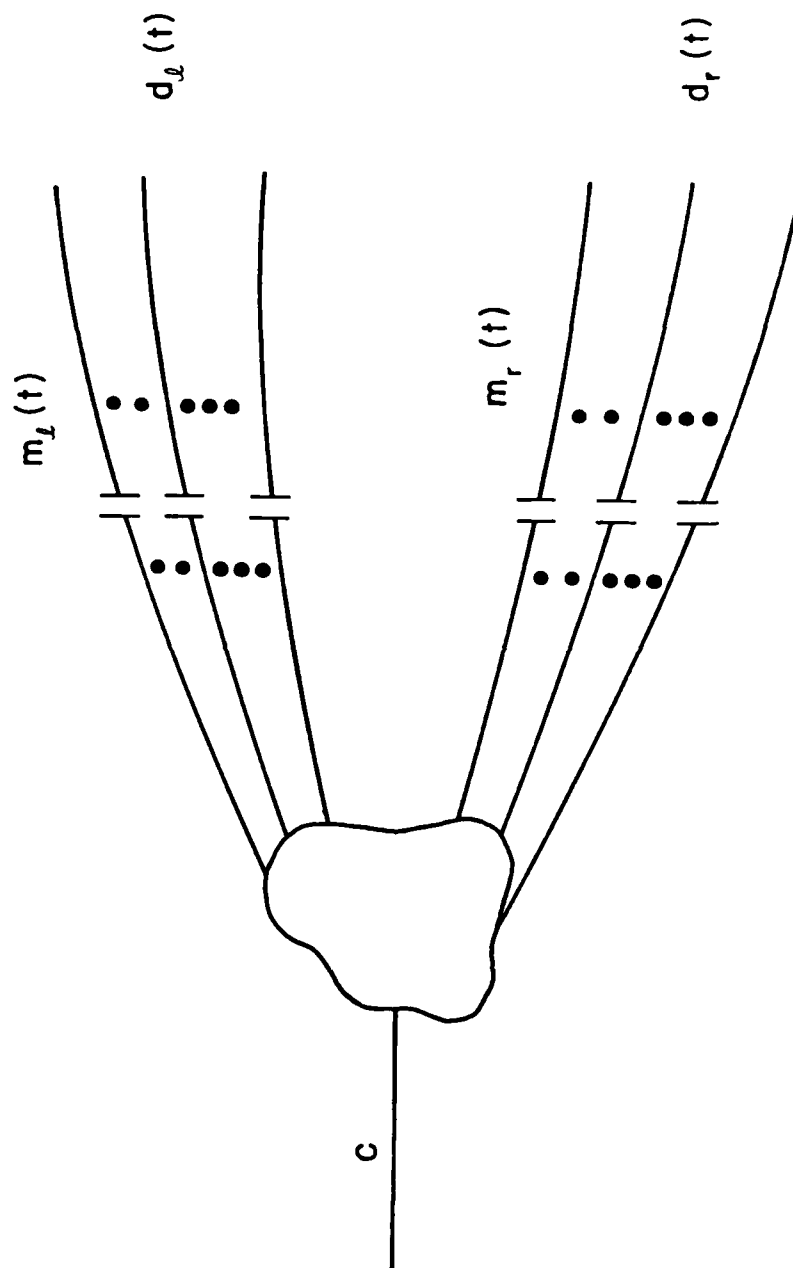
(a) NR

(b) BD

(c) MD

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